ON THE FERTILISATION OF *CLERODENDRON TOMENTOSUM*, R.BR., AND *CANDOLLEA (STYLIDIUM) SERRULATA*, LABILL.

By Alex. G. Hamilton.

(Plate II.)

Clerodendron tomentosum, R.Br.

(Pl. II. figs. 1-2.)

My attention was first drawn to the method of fertilisation of this plant by the fact that a cluster of flowers on my table, though always deliciously scented, gave off a much stronger odour in the evening. This led me to think that it was probably fertilised by some night-flying moth. I therefore studied the development and structure of the flowers with a view to discovering if my theory was correct, and with the following results :—

The flower, as seen in fig. 1, is tubular, the tube about an inch long. The five petals are only slightly irregular, the lower one being sometimes a little larger than the upper. But this is not a constant character. The colour is creamy-white—a common feature of flowers which depend on night-flying insects for fertilisation. The stamens are four in number, and much exserted—one inch or more beyond the tube, and the pistil projects to about the same distance. In the bud, stamens and pistil are compactly coiled up, and fill the interior completely. When the flower opens, the stamens gradually uncoil and straighten, and the pistil bends so as to be below them (fig. 1). The anthers do not burst till the pistil has bent, and the latter is still immature, as is shown by the bifid stigma remaining unopened. The flowers are, therefore, proterandrous. The anthers in some flowers do not all mature at once, sometimes bursting singly and sometimes in pairs, but the usual course is for all to mature and burst simultaneously. The tube produces nectar freely, but it can only be procured by an insect with a very long proboscis, and it seemed most likely to me that the sphinx or hawk moths were usually concerned in the fertilisation. After the anthers have all shed their pollen, they twist downwards, while the pistil straightens and thus brings the stigma, now open and fit to receive pollen, into the position which the stamens formerly had (fig. 2). Now this is exactly in front of the neck of the tube, so that a moth feeding on the nectar is certain, as it poises in front, to be smeared with pollen on the lower surface of the thorax and abdomen, and this pollen is transferred to the stigma when a bloom is visited which has its pistil straight and the stigma mature. Inspection of the immature stigmas when in the lower position showed them to be perfectly free from pollen. But the mature stigmas in the upper position were thickly coated with pollen, and in most cases had scales and long hairs of a moth adhering to them. My conclusion, therefore, was that the sphinx moths in extracting the nectar from blossoms in which the stamens stood out in front of the flower, became coated with the very sticky pollen ; then proceeding to flowers in which the pistil was in position they deposited the pollen on the stigma as they hovered over the flower, and so cross-fertilisation, or to use Kerner's term, allogamy, ensued. That insects are not likely to alight on the flower and so fertilise it, is evident from the fact that the plane of the petals is perpendicular to the axis of the tube, and that they curl round (fig. 2) towards the tube as the flower matures, so that there is no platform for insects to alight upon. The flowers grow in clusters, and in each cluster may be found numbers in all states of maturity. The calyx, tube and backs of the petals, stem and leaves are all covered with hairs, both pointed and glandular, and of a soft texture. This prevents ants and other crawling insects from having access to the flowers, such insects only rifling the tube of its nectar without fertilising the flower.

Having completed my theory, I took the first opportunity of putting it to the test by visiting a flowering plant in the dusk, and I then found that the method was exactly as above set forth. Numbers of hawk moths of the species *Deilephila celerio* were very busy extracting the nectar, and as they balanced on the wing above the flowers, invariably touched the anthers of those in the first stage ; or the stigma in those which had reached the second, both with their legs and their bodies. As might be expected the plant fruits freely but not invariably.

I have little doubt but that the flowers may also be visited and fertilised by the little Cobbler's Awl, *Acanthorhynchus tenuirostris*, which is very fond of visiting tubular flowers, but so far I have not observed them at it. Crowds of small moths were fluttering about the flowers, probably attracted by the sweet scent, but they did not alight: perhaps the depth of the tube and the want of a platform for resting on deterred them.

After writing the preceding, I came across the following, which has a good deal of interest as bearing on fertilisation in this manner. "Natural Science" (Vol. iii. p. 415) notices a paper by Dr. Max Schultz in Cohn's Beiträge zur Biologie der Pflanzen (Vol. vi. p. 305) "On the movements of the stalk and flower, of *Cobœa scandens*."

The flowers are proterandrous and the two upper stamens shed pollen first, the anthers standing up before the entrance to the flower, and then bend downwards out of the way. Then the three lower anthers take up the same position and open, afterwards bending downwards, while the style takes the position formerly held by the anthers, and the stigmas unfold.

After reading this, I watched a plant of *Cobœa* in flower, and was struck with the similarity of the process to that in *Clerodendron.* Although Dr. Schultz (as quoted) says that two anthers open first and then the other three, I noted that in my plant the anthers frequently opened singly, or irregularly as in *Clerodendron*, or all at once.

The notice concludes with the following words :—"These movements of the flower and its stalk are, perhaps, a device for ensuring self-fertilisation where cross-fertilisation by insects has failed. They occur in any case, whether pollination has taken place or not." With my experience of *Clerodendron*, I should say that they undoubtedly point to cross-fertilisation by a flying insect; but I am bound to admit that I have for some two months past watched *Cobœa* for hawk moths every evening, and have never seen one approach it, although they were busy on some *Lonicera* twenty feet away. The flowers were, however, much frequented by bees in search of pollen, and often bear fertile seed, but they often fail. The scent in the flowers at the first stage (at which time the blossom is greenish) is said to be pungent and disagreeable, and in those in the second stage strong and sweet. But, so far as I have observed, the scent is strong and disagreeable at all stages. These differences, however, may be due to the plant growing in a different soil and climate.

Candollea (Stylidium) serrulata, Labill.

[*C. (S.) graminifolium*, Swartz.]

(Pl. II. figs. 3-9.)

The plants of this genus are well known for their irritable column, which springs across the flower on the slightest touch. The purpose of this movement has long been supposed to be connected with the fertilisation of the flower, but I have been unable to find any record of the method by which it secures that end. I therefore hope that the results of my study and observations of the species named may be of interest.

The flowers are strongly proterandrous. The filaments of the stamens and the pistil are connate, forming the sensitive column. In the bud and the earlier stages of the flower, the anthers lap over and conceal the stigma, which is then small, green, and immature (fig. 3). They gradually open, and the pollen lies loose in them and is shed. When they are quite empty they wither rapidly, and the stigma begins to grow out. It soon becomes mature and fit for the reception of the pollen, and is then oval, cushion-shaped, and covered closely all over with fine short hairs (figs. 5 and 6), so that it is not unlike a hair-brush with a curved surface. The corolla consists of five petals uniting in a tube. Four of these have their free extremities extended in a plane at right angles to the tube, and at the mouth of the tube each has a variable number of appendages (fig. 9) forming a corona, and so arranged as to leave an opening at what I may call the front of the flower (fig. 4). The fifth petal (labellum) bends down along the tube, and has a projection at each upper angle, evidently the same as those on the upper petals. At first this is glandular, shining, and soft, but on the flower opening the glands disappear or coalesce so as to make the surface level and smooth, and the texture becomes hard and leathery. The column grows out of the tube and then bends over the neck and downwards between two of the upper petals, lying between the appendages of the labellum, and along the surface of it (fig. 3). It then bends upwards and outwards with a slight twist. The first bend over the tube is the hinge on which the column bends when moving, and is thicker and wider than the parts above and below. It also has transverse ridges at this point, which are coloured pink or crimson, while the other parts of the column are greenish or brownish-green. The whole of the flower-stem, the calyx, and, to a slight extent, the backs of the upper petals are covered with sticky crimson-headed glandular hairs or trichomes (fig. 8), the object of which is evidently to prevent small crawling insects gaining access to the flower and robbing the tube of its nectar, without any advantage to the plant. The trichomes wither on the older flowers and capsules when the necessity for them has passed away.

The flower is fertilised by insects, and it is not self-fertile, as may be seen from capsules withering from want of fertilisation, while in a spike of flowers one or two may sometimes be fertilised between flowers above and below which are not.

The method of fertilisation is as follows :—Any insect such as a bee, visiting the flower, selects the side where is the widest opening between the petaline appendages; this is exactly opposite the hinge or first bend of the column (*a*, figs. 4 & 5), and this bend is the point of greatest irritability. As the insect passes its proboscis down the tube, it inevitably touches the sensitive spot, and the column immediately flies over, the gynæcium striking the bee (if of the ordinary size) on the thorax. If the column be at the first or or pollen-bearing stage, the pollen is deposited on the bee's thorax, where it clogs the hairs. When the insect has completed its work at the flower it moves off, and to do this, it has to come out sideways on account of the way it is clasped by the column ; in this movement the pollen is further brushed out of the anther cells by the hairs on the bee's back. If the insect then visits a flower in which the pollen is all shed and the stigma mature, the same action of the column occurs, but in this case the sticky hairs of the stigma act as a brush to remove the pollen from the bee as it moves off sideways. Consideration of the structure and action of the flowers leading me to form the above theory of its mode of fertilisation, I experimented with flies, but they were either too small or would not go into the flower properly. I therefore went to a spot where the plants were fully in blossom, and soon observed a small native bee working at the blossoms. But on account of its small size it was not effectual—the column striking beyond the insect. I noticed, however, in this instance and with other insects, that the sudden blow from the column did not startle them at all, so that they are evidently accustomed to it. My friend, Mr. J. D. Cox, who assisted me in the field observations, called my attention to a hybrid Italian bee flying about the blossom spikes, and we soon had the pleasure of seeing the bee going to the open side of the flowers. On its inserting its proboscis into the tube, the column at once flew over, and where the anthers were not empty, a little cloud of pollen was seen to fly from the force of the blow. Where the stigma was mature, an examination of it afterwards showed pollen on the surface. We watched the insect visit a large number of flowers, always acting as described. It invariably visited the lower flowers in a spike first, and as these are always more advanced than the upper, and have the stigmas mature, there was little probability of any blossom being fertilised with pollen from the same plant. I then captured the insect, and found it covered with pollen of *Candollea*, and I could not afterwards detect that of any other plant under the $\frac{1}{4}$ inch power of the microscope. I might remark that, as Sir John Lubbock states, bees almost always keep to one species during a trip, but I am able to say that this is not invariable. I have several times seen a bee visit a number of different species of plants, and belonging to totally different natural orders, one after another.

In many flowers, the column had been sprung previous to the bee's visit, and in getting into position to search the tube the insect always rubbed its back against the gynæcium. If in any of these the stigma was mature, it would result in fertilisation just as certainly as if the column had struck the bee. Some columns with the stigma mature I noted standing for a long time without returning, and if an insect seeking nectar brushed against them, fertilisation would ensue if there was pollen on its back. I should not be surprised to learn that an unfertilised column at last lost its sensibility and stood in the sprung position to give the flower a last chance of receiving pollen. But I was not able to make any certain observation of the fact.

It seems important that the insect should be of such a size that the gynæcium should strike the upper surface of the abdomen or the thorax, and this requirement is fulfilled by many native bees and pollen-feeding flies.

Observations and experiments revealed the following facts :— The action is most vigorous on a warm dry day. On a cold day many columns will not respond to a stimulus, and others do so very slowly. Dr. Woolls remarks :—" This [the action of the column] does not take place in moist weather."* I found, however, that most columns would respond to a stimulus on a warm moist day, but on a cold day whether wet or dry, they remained inactive. The column below the hinge, the anthers and the stigma are not sensitive or do not transmit a stimulus, if gentle.

* Lectures on the Vegetable Kingdom, p. 100.

But a rough touch causes action immediately. This is probably due to the roughness moving the sensitive spot. But if touched ever so gently at this point, the column acts, if it be not in a sluggish condition from the effects of weather or previous action.

When an active plant is sprung, the column remains reflexed for a period varying from 2 minutes to 1 hour. The more usual time is from 10 to 20 minutes. The column then begins to return to its normal position, at first by a series of short jerks, till it is perpendicular to the plane of the petals, and then by a slow gliding movement, which is very plainly perceptible in a vigorous flower, till it has reached its normal position. After recovery, it will not respond to a stimulus for a variable length of time, the shortest observed being 20 minutes, and the longest 4 hours. It is as sensitive at night (up till midnight at least) under ordinary circumstances as in the daylight.

When the flowers have been fertilised, they retain their sensitiveness for a period varying from 4 to 24 hours. Sometimes a fertilised flower, if touched, acts vigorously and then moves back till the column is perpendicular, and then remains in that position finally. Soon after the loss of irritability, the petals wither.

A smart current of air driven on the flower by the lips causes the column to act, and doubtless the wind has the same effect. This probably arises from the wind moving the irritable point. But this would not matter, for a sprung flower, as already pointed out, would reach the back of a suitable insect visiting the flower while the column was reflexed, and would perform its proper function of depositing or receiving pollen.

The flowers vary as to the number of appendages on each petal —one, two, or three; and number of petals—sometimes six. But in all cases the front of the flower is the side most easy of access to insects.

There are two points in the structure of the flowers of which I could not make out the utility. The first is the object of the beaded hairs on the gynæcium (fig. 3); these appear to be appendages of the anthers, and wither as the anthers do. The other is the rudimentary petal or labellum folded down the sides of the tube. The two horns on this are manifestly homologues of the coronal projections on the ordinary petals. As the column in its ordinary position lies between these horns, they may be guides to lead it into its proper place as it returns after action. But on several occasions I saw the style get outside the horns.

I was not able to try the effect of chloroform vapour on the plants; tobacco smoke did not affect the column in the slightest either way. Darwin's experiments on Orchids seem to show that the vapour of chloroform is inert as regards sensitive organs of plants.

The plants are gregarious, which must be a decided advantage to them as insect-fertilised. I collected some specimens remarkable for size and number of flowers. Three were specially fine. No. 1 was 3 feet 5 inches high and had 70 flowers, 36 fertilised and capsules swelled, two with withered and empty capsules, 13 open flowers and 19 buds. No. 2: 2 feet 9 inches high, with 52 flowers, 10 fertilised, 23 open flowers and 19 buds. No. 3: 2 feet 6 inches high, 50 flowers, 16 fertilised, 20 open flowers and 14 buds.

In conclusion I would draw the attention of members who have facilities for laboratory work, to the interest which would attach to a series of sections, transverse and longitudinal, of the column, especially of the hinged part, which is the seat of irritability, and which shows, outwardly at least, a differentiation of structure in the presence of strongly coloured ridges across the column.

REFERENCES TO PLATE II.

Clerodendron tomentosum, R.Br.

Fig. 1.—Flower in first or male stage; *a*, anthers, *s*, stigma unopened (× 2).

Fig. 2.—Flower in second or female stage; *a*, anthers curled out of way, *s*, stigma in position and open (× 2).

Candollea (Stylidium) serrulata, Labill.

Fig. 3.—Flower from behind (× 2).

Fig. 4.—Flower from front, showing opening for insect; *a*, sensitive hinge of column (× 2).

Fig. 5.—Anthers concealing stigma (× 5).

Fig. 6.—Stigma from above, anthers withered (× 5).

Fig. 7.—Side view of stigma (× 5).

Fig. 8.—Trichomes on stem and calyx (× 20).

Fig. 9.—Appendage of the petals (× 5).